X. *Morphological Notes bearing on the Origin of Insects.* By J. Wood-Mason, F.G.S., F.L.S., F.Z.S., Deputy Superintendent, Indian Museum, and sometime Professor of Comparative Anatomy, Medical College, Calcutta.

[Read May 7th, 1879.]

1§. Their position relative to the eyes* and mandibles seems to point to the antennæ of *Machilis* as being homologous with the antennæ (III) proper of Crustacea. These appendages are, in *M. maritima*,† composed, as usual, of a peduncle and of a flagellum: the former consists of a single joint, which is rather broader than long, and slightly enlarges from its insertion to the end of the basal third, where it is thickest, and where a conspicuous sutural mark shows that it is made up of two primitively distinct and separate joints; near its apex, on the inner and inferior side, arises a short conical process, terminating abruptly in a small blunt papilla, from which spring one or two hairs. When the insect is at rest, the antennæ are laid back upon the sides of the thorax, bending at the junction of the peduncle with the setaceous subsegmented flagellum: the first joint of this—little more than half the thickness of the peduncle—is of uniform breadth throughout, almost twice as broad as long, its breadth being to its length as 8 : 5 about, and it is slightly excavated at that part of its wall which, when the antennæ are directed straight for-

* Immediately beneath each of the eyes is a conspicuous black and rounded ocellus-like elevation, which may represent the simple eyes of *Peripatus;* they are clearly not identical with the fenestræ of *Blatta*, which are, perhaps, the scars of the lost antennules. It seems to me doubtful whether the antennæ of *Blatta* and *Machilis* homologize with those of *Glomeris*, in which, while the antennæ occupy the place of the fenestræ, a pair of horse-shoe shaped membranous depressions, singularly like the antennary fossæ of a cockroach, is in the position of the antennæ in *Blatta*.

† For the benefit of any one who may wish to obtain specimens of this primitive form of insect for dissection, I may state that the species abounded at the end of April and the beginning of May, 1878, on the huge fallen blocks of Corallian rock that thickly strew the beach under the ruins of Sandsfoot Castle, and on the slabs of stone from the Cornbrash cliffs of the backwater, near Weymouth. All these ancient forms have a remarkably wide distribution.

wards, comes into apposition with the papilla-bearing process of the peduncle.

In an Indian species of *Lepisma* the antennæ are furnished, at the extremity of their two-jointed peduncle, with a minute movably-articulated appendage, exactly corresponding in position to the papilla in *Machilis*, and as firmly chitinized as the basal joint of the flagellum.

Let us see what light lower, that is to say, less modified, air-breathing arthropods throw upon the nature of these rudiments in the *Lepismatidæ*.

It will, doubtless, be in the recollection of many of the members that Sir John Lubbock exhibited at the November Meeting of this Society, in 1866, and shortly afterwards very fully and carefully described in the 'Transactions of the Linnæan Society of London,' a remarkable addition to the fauna of these islands in a new form of Myriopoda, the most striking morphological feature of which undoubtedly is the possession by it of biramous antennæ. In *Pauropus*, as this curious little creature is named, in allusion to the paucity of its locomotor pairs of members, the two antennary branches, one supporting one and the other two many-jointed flagella, are themselves supported upon a peduncle of four joints—a number which has, probably, resulted from the secondary segmentation of two primitive joints, as, in fact, is indicated in Lubbock's figure of a larval stage, though nothing is said about the number of the joints in the accompanying text.

Sir John Lubbock did not fail to remark the singularly close resemblance which the antennæ of *Pauropus* bear to those of many Crustacea; "in their bifid character, and in the possession of long, jointed appendages," they "offer," he says, "peculiarities which can be found, so far as I am aware, among no other terrestrial Articulata, and which remind us strongly of the types presented by the antennæ of certain Crustacea;" and other writers, such as Rolleston, have recognized in them a peculiarity by which "a very distinct affinity is shown to exist between Myriopoda and Crustacea."

If for the movable appendage present in the Indian *Lepisma*, and for the reduced representative of it in *Machilis*, were to be substituted a fully-formed flagellum, in other words, if these rudimentary structures were restored to what I believe to have been their pristine condition, it is obvious that we should then have in each case antennæ in all essential particulars like those of *Pauropus*, or like the antennæ proper (III) of such a Crustacean as

the female of the common *Cyclops* of our freshwaters, or as an ordinary Zoëa, in both of which latter, as in the larvæ of the former, the antennæ similarly consist of a proximal or basal two-jointed portion, the protopodite or peduncle, terminated by two branches, the endopodite and exopodite.

As I had good reasons for believing that the ancient, cosmopolitan, and little-modified group of the cockroaches is directly descended from some extinct form of which the *Lepismatidæ* are the only existing representatives that we know of, I thought that, by carefully tracing the development of the antennæ in some species of it, I should probably find a vestige of a second antennary branch occupying the place of the rudiments in *Machilis* and *Lepisma*. Nor have I been disappointed. In ripe embryos of *Blatta* (*Panesthia*) *Javanica*, which are still invested in a larval skin, the one, probably, that is cast by the young cockroaches at the moment of quitting the marsupium of the mother, the antennæ in all essential particulars resemble those of *Machilis*, consisting of a many-jointed flagellum borne upon a two-jointed peduncle, from the apical joint of which arises a relatively huge somewhat compressed conical process, in the precise place of the papilla-bearing tubercle in *Machilis*. This process seems quite as entitled to be considered a distinct part as is the simple one-jointed antennary (III) endopodite of many Zoëas. It is probably cast off with the skin the young insect sheds on leaving the body of the mother, and to which it appears to belong; be this as it may, no vestige of it is to be detected in the smallest active 'larvæ' of the same species yet examined by me.

There seems to me little doubt that we have here to do with an ancestral phase of the antennæ, a phase in which those appendages each consisted, to use the terminology employed in carcinology, of a proximal two-jointed protopodite, carrying at its extremity a long many-jointed exopodite, and a short and simple rudimentary representative of an endopodite. The ancient condition of things, of which we thus get a passing glimpse in the embryonic history of this cockroach, may be presumed to have been inherited from some extinct form closely resembling the much less modified *Lepismatidæ*, in which also an endopodite is present, though it is reduced to the merest rudiment. In short, in the lowly *Pauropus* we have antennæ with two fully-developed branches; in the higher *Lepismatidæ* the inner of these two branches is reduced to a mere

rudiment, which, however, persists throughout life; and in the still higher cockroach even this is absent in adult life, being only seen as a transient condition in the embryo.

Fig. 1.

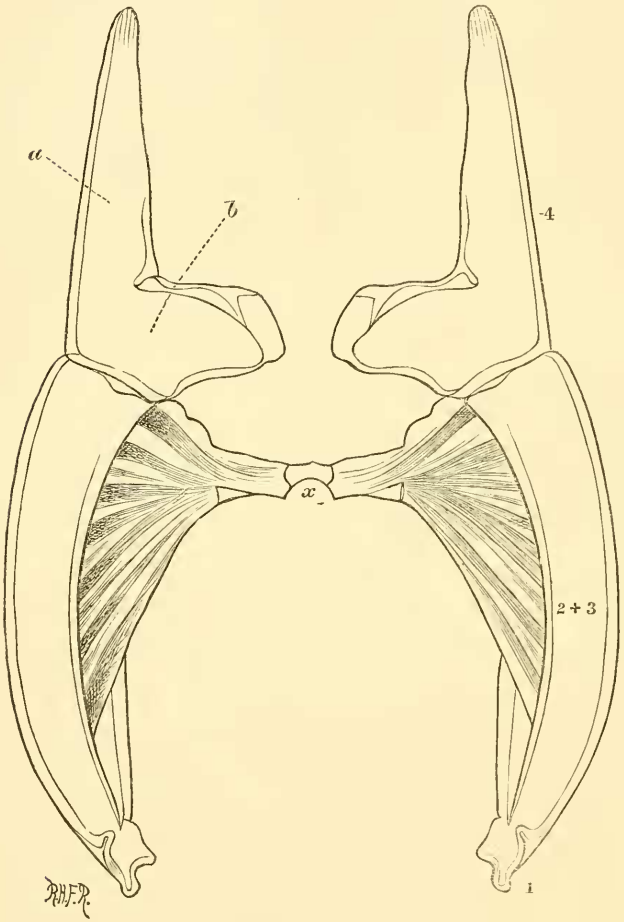

Fig. 1. *Machilis* (*Petrobius*) *maritima*. Mandibles, viewed from above; *a*, exopodite, *b*, endopodite, 1, 2 + 3, 4, the three joints, *x*, median chitinous plate to which the great flexor muscles are attached.

2§. The mandibles (fig. 1) of *Machilis* have been figured in outline, and briefly described by Sir John Lubbock, but both he and all other writers have apparently overlooked

the important fact that these appendages are jointed and articulated to the head just as in the Chilognathous myriopods. The joints, however, are not movable, but, on the contrary, quite stiff, the process of modification suggested below having apparently already commenced. The posterior ball-shaped condyle of mandibulated insects, clearly foreshadowed in the myriopod, is here fully formed and provided with a distinct neck; it is a process of the minute basal joint (1, fig. 1), which is indicated by a distinct inflection of the integument; the second joint (2 + 3) answers to the second and third in the myriopod; and the third and apical free one (4) has a well-developed molar tubercle at the base of its long, knife-shaped incisive process, which is obscurely toothed, or, rather, crenulated, on the inner extremity; it is marked off from the preceding joint by a conspicuous constriction as well as by a circumferential inflection of the integument. The two basal joints form almost the whole of the side of the head, as in the *Chilognatha*, that is to say, roughly speaking, the part corresponding to the so-called 'gena' in *Blatta;* they terminate where the apical joint begins, at a point approximately answering to the position of the 'ginglymus' in *Blatta*. The great flexor muscles are inserted into the inner face of the outer wall, and pass thence through a cleft in the opposite wall of the second joint to be attached to a median chitinous plate; so that, just as in Chilognathous myriopods, the two mandibles come away attached together when it is attempted to dissect out either one of them.

In the ripe embryos of '*Blatta*' (*Panesthia*) *Javanica* previously alluded to, two deep folds* are to be seen in the integument of the 'back' of the mandible, between the base of the apical crushing and cutting part of the appendage and the condyle; they pass across both sides of

* Folds not of the larval skin previously referred to, but of the integument of the enclosed appendage, in the interior of which the definitive non-jointed mandible is plainly visible by transmitted light, and is almost ready for use. In all the ametabolous Insects, the mandibles and the claws of the feet are never for a moment useless to their possessors, but are continuously in use from birth to death, the portion of the thin exuvium that covers the parts being worn away by use, and the new jaws and claws exposed, before the moult takes place. In both the species of *Peripatus* dissected by me, not one only but two pairs of these reserve jaws are present, that is to say, there are two claws in different stages of development in the interior of each of the functional ones. This phenomenon appears to be universal in Arthropoda, Thorell ('Monograph of *Argulidæ*') having observed it in *Argulus*, and Hollis ('Journ. Anat. and Phys.'), in some of our indigenous terrestrial Isopoda.

the mandible more or less distinctly, and the apical one of the two is continuous with the outer margin of the fleshy setulose flap that projects from the inner margin of the jaw in all *Blattidæ;* moreover, the part from which the ball-shaped condyle is given off is indicated as a separate piece by a distinct inflection of the integument; so that, counting this last as the first, the two folds as the second and third, and the part of the mandible that succeeds these, and that becomes firmly chitinized at the same time as the condyle, namely, the cutting and crushing apical part, as the fourth joint, we have indicated in the mandible of this embryo cockroach the same number of joints as in that of Chilognathous myriopods, or one less than in that of *Machilis,* in which the second, answering to the second and third of the myriopod and to the two folds in *Panesthia,* may have resulted from the coalescence of two primitively distinct joints.

The setulose flap above-mentioned seems rather to be a mere process of the third segment than a distinct part, such as an endopodite, and it is, besides, quite unrepresented in the far less modified *Machilis;* its apex, in embryo as in adult, is received into a notch specially provided for it in the proximal end of the molar process. It is present as a minute, white, fleshy, naked, and obviously useless rudiment in the nearly related and only slightly more specialized *Mantidæ*, but, so far as I have yet discovered, in no other Orthoptera,* nor in any Neuroptera, except, perhaps, *Termes.*

In both 'larvæ' and adults of *Panesthia Javanica* a faint groove crosses the 'back' of the mandible at the base; in this Oriental species, eight abdominal terga only are in both sexes visible from above without dissection; but some South American forms are so far less modified than this as to have, in the male, at any rate, ten, the full number of terga externally visible, and it is a significant fact that, in the only one of these I have as yet had an opportunity of examining, the groove is deeper, and at bottom of much lighter coloration than the surrounding chitine. This groove appears to be the remains of the joint between the third and apical segments of the formerly four-segmented mandibles.

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* Of these, the *Phasmidæ*, at any rate, would appear to differ from the *Mantidæ* and *Blattidæ* in that, in the female, the opening of the urogenital chamber lies between the tenth tergum and the eighth, instead of the seventh, sternum, and in the male between the tenth tergum and the tenth, instead of the ninth, sternum.

After prolonged study of numerous dissections and preparations, I have arrived at the conclusion that the mandibles of *Blattidæ* are compound structures, each made up of three (or four) such joints as are to be seen in *Machilis;* and I believe that the process of modification by which the head and mandibles of such an insect as *Machilis* have become converted into those of *Blatta* may have been somewhat of this nature; the basal joints have gradually shortened and coalesced with one another until little more was left of them than the ball-shaped condyle; *pari passu* with this change the walls of the head have gradually completed themselves behind the shortening and retiring basal joints of the jaws, so as eventually to form a 'gena;' and finally, a 'ginglymus' articulation was formed by a process sent off from the front of the head to meet a cupped process of the base of the mandible* of the same side.

3§. Are the mandibles of insects and myriopods, like the jaws of *Peripatus*, modifications of walking-legs? I think not. In the cockroaches, a notch at the extremity of the mandibles on the inner side sharply divides the crushing and cutting portions of those appendages from one another; in the embryos a curvilinear sutural mark extends from the bottom of this notch, and separates the two parts off from one another still more definitely; this is seen better marked in all the species of *Lepisma* (see Lubbock's figure of the mandibles of *L. saccharina*), a form in many respects intermediate between *Blatta* and *Machilis*, and in some of the species of which the apical portion of the mandible closely resembles that of *Blatta*. In *Machilis*, the notch becomes a deep fork, widely separating the two parts, and from its bottom there extends basewards a distinct inflection of the integument. This peculiar feature in the structure of the apical joint seems to me only explicable on the hypothesis that the mandibles of these insects and of myriopods have resulted from the direct modification of such a biramous appendage as is seen in the earliest (*Nauplius*) condition of many crustaceans, the two or three basal joints attached to the head representing the protopodite, and the molar and incisive

* The 'ginglymus' is still incomplete in the ripe embryos with which I have worked, and I do not think it is completed till after birth, probably not till the first extra-ovular moult has taken place and removed all traces of segmentation in the mandibles. The embryonic development of the mandibles in *Blatta* repeats the historic development perfectly.

portions of the terminal free joint, the endopodite and exopodite respectively of the embryonic crustacean mandible. If the view here suggested be correct, the possibility of the occurrence of a mandibular palp in insects and myriopods is altogether excluded, the extremities of both the branches of the primitive member entering into the formation of the functional jaw; and the peculiar appendages found on the inner side of the mandibles in many Coleoptera acquire a definite morphological signification, I refer to the 'prostheca' of Kirby and Spence, and to the structures homologous with it in beetles other than *Staphylinidæ*. In the 'Devil's Coach-horses' (*Goërius oleus*), in *Staphylinus erythropterus*, and other 'Rove-beetles,' and in the sub-aquatic *Heteroceridæ*, no molar process is developed; but in its place, movably articulated to the jaw, is a membranous ciliated appendage not unlike the endopodites of *Scolopendrella*. I am convinced that this is an endopodite, and that it answers to the molar branch of the jaws in *Blatta* and *Machilis*. It has its homologue in the diminutive *Trichopterygiidæ* in the firmly-chitinized quadrant-shaped second mandibular joint, which is used in a peculiar manner * in crushing the food. It is represented by the membranous inner lobe of the mandibles in the Goliath beetles of Southern Asia, which inner lobe frequently becomes indurated and grooved internally so as to function as a feeble crusher of the soft food of these insects, in many *Phytophaga*, and in *Donacia*, which is considered by some to bridge the interval between these last and the longicorns; in some of which, as, for instance, in *Batocera*, a wrinkled papilliform scar remains to mark its former presence.†

4§. One of the most interesting and remarkable features in the whole organization of the Thysanura is the presence of abdominal appendages, which, in *Machilis*, are movably articulated to the hinder margin of the sterna of the eight antepenultimate somites, a pair to each somite. Sir John Lubbock was, I believe, the first to put upon record the important fact "that each of the four posterior legs bears an appendage on the basal segment closely resembling the

* Mathews, 'Monograph of Trichopterygiidæ.'

† It is probably represented also by the movably-articulated and firmly-chitinized appendage, shaped like the terminal joint of one of the palpi, which I have discovered on one of the mandibles in Australian, Asiatic, African and South American *Passalidæ*. But in this case the large molar surface of the mandible must be a process of the cutting portion.

eight anterior ventral appendages;" but the precise position on the legs which these appendages occupy appears never to have been indicated; they are articulated to the upper

Fig. 2.

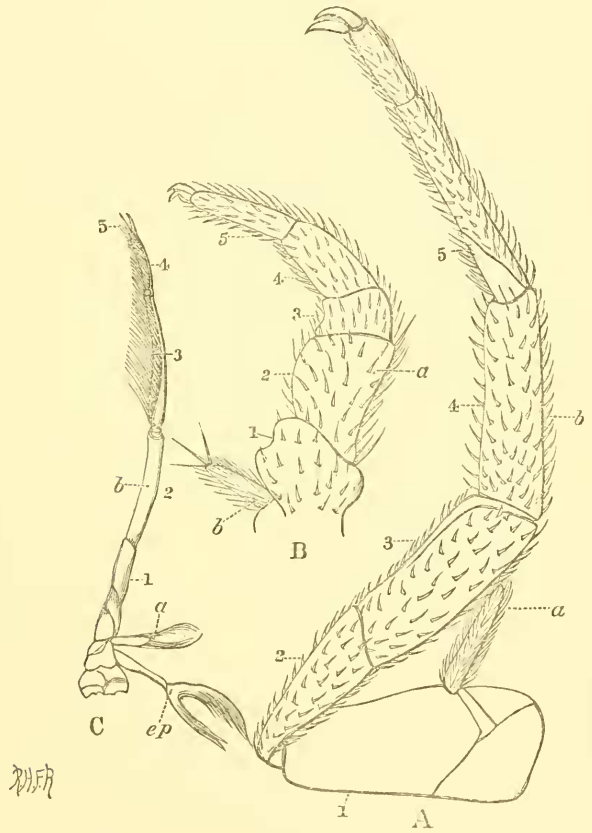

Fig. 2. (A) Metathoracic leg of *Machilis maritima;* (B) leg of *Scolopendrella* sp.; (C) fifth thoracic appendage (XI) of *Penëus Dobsoni; a,* exopodite; *b,* endopodite; *ep,* epipodite; 1, 2, 3, 4, 5, the five joints of the ambulatory branch of the limb, which in (A) and (C) is here considered to be an endopodite, but in (B) an exopodite.

and outer edge of the legs at a point where a distinct angulate suture indicates that the coxa is composed of

two parts, a long and broad distal one—the true coxa—and a short proximal one, divided by an evident suture into two. It is clear that these answer to the distal of the two sclerites which are interposed between the coxa and the sternum in *Blatta*, and which, in my opinion, are both basal joints of the leg. In *Machilis*, owing to the softness and delicacy of the integument at the setting-on of the legs, and to the presence of the long pleural prolongations of the thoracic terga, a third sclerite, answering to the basal one in *Blatta*, is difficult of demonstration; but in *Lepisma*, a leg, when torn from its attachment, carries away with it three short joints, the basal one of which, as it lies *in situ*, is overlapped by the triangular part of the sternum. Some of the least modified of *Blattidæ* have preserved almost perfectly the condition of things seen in *Lepisma;* but in the more modified forms, such as *Panesthia*, the basal sclerite of the legs is, as often happens in arthropods, immovably articulated, though not confounded, with the sides of the sternum, while the two distal sclerites are ankylosed together and show a tendency to become united to the coxa; the consequence is, that the leg bends at its base, not between the sternum and its true basal joint, but between this latter and the following joint. The appendage, then, in *Machilis* is articulated to the outside of the limb at the junction of the three-jointed basal with the five-jointed apical portion; it has, in fact, the same relation of position to it as has the precisely similar, and, as I believe, morphologically identical, *exopodite* to the five-jointed *endopodite* and to the *protopodite* in such a crustacean as *Penëus;* the only difference being that *Machilis* appears to have one more joint in its protopodite—a difference which may be accounted for on the supposition that *Machilis* is descended from some crustacean form* in which a three-jointed protopodite is found.

"The basal segment [of the maxillary palpi] has a process regarded by Latreille as representing the cylindrical appendage of the posterior legs."† I cannot, however, regard this as anything but a mere process of the basal joint; a comparison of the two posterior gnathites

* The *Phyllopoda*, some of the existing members of which have a distinct head like the insects and myriopods.

† Lubbock, 'Monograph of the Collembola and Thysanura,' 1873, p. 202.

and of the thoracic sternum and its appendages of *Machilis* with those of *Blatta* and *Lepisma* appears to me rather in favour of the view that the thoracic exopodites of the former, if represented at all in its maxillæ, are represented by the whole palp in both pairs, and that the outer of the three lobes into which the less modified second pair is on each side divided perhaps answers to a thoracic leg, while the middle and inner ones are processes of the two terminal joints of the protopodite, the first joint * of this having coalesced with its fellow of the opposite side to form the great azygous basal plate, the 'submentum' of *Blatta*.

The presence of a similar appendage on the inner, instead of the outer, side of the very base of the first free joint † of all the legs except, according to Lubbock, the first pair in the myriopod genus *Scolopendrella*,‡ suggests the suspicion that the limbs of myriopods are not strictly homologous with those of insects, but that they correspond with the rudimentary appendages of *Machilis*, and are consequently exopodites, the appendages of the legs in

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* The following pair or pairs of sclerites have not coalesced to form a 'mentum' as in *Blatta*, the two inner lobes of the jaw of which have been lost in the greater coalescence of parts that has taken place therein, the outer one alone remaining as the paraglossæ.

† This is here the fifth from the distal end of the limb. Two short joints, represented in this small and excessively-fragile creature by two scarcely perceptible folds, seem to be interposed, as in *Scolopendra*, between this first free basal joint and the sternum, and the appendage springs from the notch between the two folds and the first free basal joint of the limb. *Scolopendrella* differs from all myriopods known to me, and agrees with *Peripatus* and all insects in having legs terminated by two curved claws. In many of the legs of my specimens of *Peripatus* (*P. Moseleyi*, with 21—22 pairs of walking-legs, from S. Africa), I find, between the first joint and the foot-cones, on the under or inner side, a wart larger than the rest and terminating in a smooth and very low papilla, distinctly marked off from the wart by a circular groove. It occupies the same position relatively to the leg, and may represent the endopodite of *Scolopendrella*. *Scolopendrella* has very remarkable antennæ; they may be compared each to a series of glass cups strung upon a delicate hyaline and extensible rod of uniform thickness throughout; so that, like the body of the creature, they shrink enormously when the animal is irritated or thrown into alcohol, and they then possess scarcely two-thirds the length they have in the fully-extended condition, their cup-like joints being drawn close together, one within the other. *Peripatus*, *Iapyx*, many (if not all) Homoptera, and the S. Asiatic relatives of our common *Glomeris* have all more or less extensible antennæ.

‡ This curious myriopod is common all over Painswick Hill, Gloucestershire, where it lives beneath stones which have long lain, as their weathered or lichen-covered tops testify, deeply buried in the turf. The rarer and still more fragile *Campodea* lives in similar situations. I obtained all my specimens of both genera in the months of April and May.

Scolopendrella representing the legs of insects, which would appear to be endopodites.*

The appendages of the legs, both in *Machilis* and *Scolopendrella*, appear to be quite immovable, and I feel sure that they are nothing but functionless rudiments. Those of the abdomen, in *Machilis*, on the contrary, are movably attached; the last and longest pair of them is invariably used in ordinary locomotion, and it is by their aid, at all events, that the sudden and powerful forward leaps † which the creature executes on being touched are effected; the rest, though they frequently move forwards and backwards with the hindermost pair, only succeed in planting themselves upon such projections of the surface over which the insect is passing as happen at the commencement of the strokes to come within reach of their shorter length. In their position of rest in the living insect they all slope downwards and backwards; but when a stroke is to be made they must be brought from this position to one in which they slope in the opposite direction, that is to say, forwards.

These appendages are commonly said to be attached to the posterior margin of the sternum, but a comparison of the sternum and appendages of the second abdominal somite with those of the metathorax shows that this is not the case. In *Machilis*, or, better, on account of its larger size, in such a cockroach as *Panesthia javanica*, the metathoracic sternum is made up of a short and soft anterior portion covered by the preceding somite, and of a hard and triangular posterior portion, to each side of which are articulated the two short basal joints that carry the five-jointed limb. Let us suppose the two limbs to be altogether aborted, rudimentary exopodites to be added in their proper place, and the two basal joints to be indistinguishably fused together, but to remain limited off from the sternum by a distinct suture and divided from their

* It should not be forgotten that, in the Mysis-stage of some prawns, it is the endopodite, and not the exopodite, of the thoracic members which is small and simple:—"Die funf neuen Fusspaare sind zweiästig, *der innere Ast kurz, einfach,—der äussere länger, um ende geringelt*"—Fritz Müller, 'Für Darwin,' S. 41, fig. 31. If such a long exopodite were to grow up into a five-jointed ambulatory limb, the simple endopodite persisting, we should have precisely the condition of things we see in *Scolopendrella*.

† Supposing that all animals which now fly are descended from ancestors that jumped, it is interesting to find this wonderful saltatorial ability and the beginnings of wings in the Crustacean-like pleural prolongations of the thoracic terga of these 'Urinsekten.'

coalesced fellows of the opposite side by a fissure extending to the apex of the triangular sternum; finally, suppose the integument of the limb-bases internally to the exopodites to be pierced by apertures leading into glandular pouches; and we shall have arrived at an understanding of the structure of the second abdominal sternum (fig. 3) in *Machilis;* the second abdominal somite, in fact, closely resembles the metathorax deprived of its five-jointed limbs. The abdominal appendages of *Machilis,* therefore, are not articulated to the sternum but to a sclerite, which represents the basal joints of a thoracic limb—to a protopodite, in fact. In the somites anterior to the eighth the endopodites appear to be entirely absent, but in the eighth and ninth of the female they are represented by the long, jointed styles, two to each somite, constituting the four elements of the ovipositor (figs. 6 and 8).

In *Lepisma,* the appendages of the abdominal somites anterior to the eighth are represented, as Lubbock correctly considers, by a group of stiff yellow setæ; internally to these, on each side, is, according to the same author, "a second similar group nearer the median line, which appears to represent a second process, formed by a prolongation of the ventral margin of the penultimate segment." It is clear that each of these more mesial pairs of fringes are the remains, not of the prolongations referred to, but of a pair of such rudimentary movable endopodites as I find, in the male, attached to the upper (dorsal) side, close to the inner margin of the prolonged protopodite (fig. 5) at about the same level as the longer and indistinctly-segmented exopodites. These rudimentary endopodites are clearly homologous with the posterior elements of the ovipositor in *Machilis* and *Lepisma.*

5§. When specimens of *Machilis maritima* are plunged into alcohol a single or a double pair of oval and pedunculated bladder-like bodies is protruded, apparently, from the posterior edge of the sternum, but, in reality, from the apex of the coalesced basal joints of the limbs (immediately internally to the rudimentary exopodites, where such are present) of each of the abdominal somites from the first to the seventh, both inclusive. When first thrust out they are as bright and, to the naked eye, as clear as little globules of Canada-balsam, but they rapidly become clouded and eventually opaque-white under the action of the alcohol. The bladders are everted glandular pouches, each provided with a powerful retractor muscle, divided

at its distal extremity into at least four branches, which traverse the glandular tissue and are inserted into the inner surface of the thin, smooth, and delicate epithelial membrane constituting the wall of the protruded bladders. Whether the bottom of the hilus-like depression seen at the extremity of each of them is prolonged into a tube opening into, or ending blindly in, the body-cavity, I have not yet been able to make out, but when the bladders are drawn in their external surfaces become the walls of glandular pouches, each opening to the exterior by a pore, which is defended by a chitinous operculum fringed with setæ on its free margin.

Fig. 3.

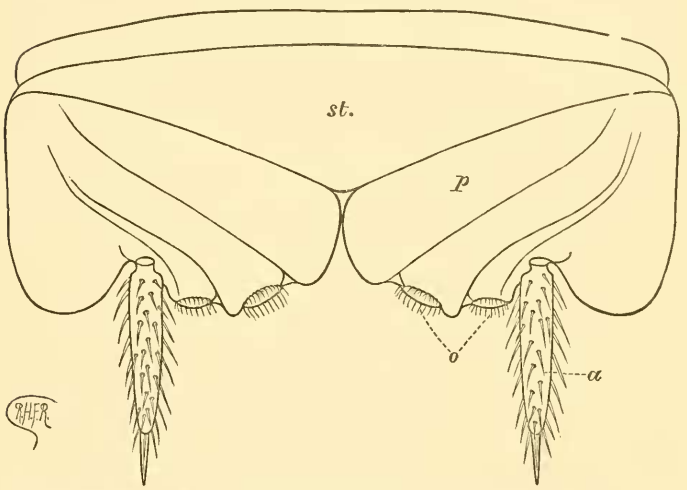

Fig. 3. *Machilis maritima;* sternum with appendages of 2nd abdominal somite; *st*, sternum; *p*, the coalesced basal joints of the right member; *o*, the fringed opercula covering the external apertures of glandular pouches supposed to be homologous with the nephridia, renal pouches, or segmental organs of worms; *a*, the exopodite, or outer branch of the member. This sternum only differs from a thoracic sternum in the absence of ambulatory legs (endopodites), and in the presence of glandular pouches.

The second to the fifth somites are each provided with four such pouches, viz., two opening close together near and internally to each exopodite; but the sixth and seventh, as also the first, which has lost its exopodites, have only a single pair.

In an inland species with short antennæ (apparently *Machilis* (*Forbicina*) *polypoda*) which I have found in considerable numbers on Painswick Hill, Gloucestershire, there is but a single pair of these pouches to each of the somites that in the littoral species has two.

These structures were first observed by Guérin,* who apparently only knew them in their everted condition in alcoholic specimens, and who, from their somewhat similar form and position, not unnaturally regarded them as branchiæ, analogous to those of Isopod Crustacea. Burmeister † objects to this interpretation, and considers that they must have some other signification, internal breathing organs — namely, tracheæ — being already present.

In *Nicoletia*, the abdominal exopodites are said by Nicolet to be "accompagnées chacune au côté interne d'un petit corps vesiculeux et ovale faisant probablement partie des organes de la respiration."‡ These are, doubtless, identical with the structures observed by Guérin and myself in *Machilis*.

Campodea§ has five or six pairs of relatively larger glandular pouches.

I am inclined to look upon these pouches as renal‖ or segmental organs, especially as I have observed, on the ventral or inner surface of all the conical foot-protuberances of *Peripatus*, in a position therefore answering as nearly as possible to that of the openings in *Machilis*, a slit-like pore, with swollen and slightly-everted mouth, leading, no doubt, into the segmental organs¶ discovered by Hutton,** and traced by him into the legs.

The recently-everted pouch in *Machilis* is covered with

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* Ann. d. Sc. Nat. 1836, p. 374.

† Handb. d. Entom., Bd. ii. 1839, p. 455.

‡ Lubbock, 'Monograph of Collembola and Thysanura.'

§ Already observed by Meinert (Ann. Mag. Nat. Hist. 1867, ser. 3, vol. xx. p. 375).

‖ It is a significant fact that no Malpighian vessels have yet been detected in any Thysanuran except *Lepisma*, in which these glandular pouches appear to be entirely absent; Meinert says, "I have failed to discover Malpighian vessels, nor do I think they exist either in *Iapyx* or in other Thysanura."

¶ The aperture of the apparently homologous slime-glands, in the embryo of *P. capensis*, occupy the same position (*teste* Moseley in Phil. Trans.).

** Ann. Mag. Nat. Hist. [Two papers on *Peripatus*, by Mr. Hutton, are contained in Ann. Mag. Nat. Hist. XVIII. pp. 361—369, and XX. pp. 81—83.—Ed.]

a film of liquid, the secretion of the gland, its microscopic appearance being precisely that of an object examined under the microscope before the spirit from which it has been taken has had time to evaporate from its surface, and a minute drop of fluid being left upon a piece of glass applied to it. In the worms the secretion of the segmental organs is carried out of the body by currents created by the cilia with which the walls of the excretory canals are clothed, but in *Machilis*, and probably in *Peripatus* also, by the eversion of the pouches, no arthropod possessing cilia on any part of the body at any period of its existence.

In the first abdominal somite the apertures of the glands are placed much nearer to the middle line than elsewhere, and it is clear that the ventral tube or sucker of the Collembola (which bear much the same relation to the Thysanura as the Brachyura do to the Macrura amongst Crustacea, or as spiders to scorpions amongst Arachnida) has resulted from the coalescence, or rather the partial coalescence, of this pair of glands, for it everywhere exhibits traces of having once been a paired organ:—"In *Podura*, *Lipura* and the allied genera, this organ is," according to Lubbock,* "a simple tubercle, divided into two halves by a central slit; in other genera, as, for instance, in *Orchesella* and *Tomocerus*, the tubercle is enlarged and becomes a tube, divided at the free end into two lobes. In the *Smynthuridæ* and *Papiriidæ* the organ receives a still further and very remarkable development; from the end of the tube the animal can project two long delicate tubes, provided at their extremity with numerous glands." Similarly, the first maxillæ in myriopods, and the second in insects, have coalesced to form a labium, different pairs of abdominal appendages, the springing apparatus of the *Collembola*, the originally paired sexual apertures, the single aperture of all insects,† &c.

The glandular pouches are absent from the two genital somites in *Machilis*, having possibly united to form the apertures and ducts of the genital and accessory genital

* Lubbock, 'Monograph of the Collembola and Thysanura,' p. 68.

† It is interesting to find in the lowest insects (Thysanura) traces of the former duplicity of the sexual aperture. Meinert says of *Iapyx*,—"The sexual orifice rests on the posterior margin of the ventral shield of the eighth ring, and the *deeply bifid* vagina of the female can be protruded from the latter;" and of *Campodea*,—"The sexual orifice is behind the eighth ventral shield, in a conical protuberance, which is simple in the male, but in the female *almost bifid*." *Iapyx* and *Campodea* are in this respect intermediate between the rest of the insects and the myriopods.

glands; however this may be, the remarkable difference in the position of the genital openings exhibited by the different groups and, very generally, by the opposite sexes of Arthropoda is intelligible on the hypothesis that all the members of the sub-kingdom have descended from some worm-like creature, provided in every somite of its body with a pair of segmental organs or nephridia, and that different pairs of these organs have, in different descendants of this hypothetical ancestor, been converted into the genital aperture and ducts.

6§. The gonapophyses of female *Blattidæ* are homologous, part for part, with the appendages of the eighth and ninth abdominal somites in the female of *Machilis*. No one has, so far as I know, ever suggested that the exarticulate setose styles (fig. 4) movably attached to the hinder extremity of the ninth abdominal sternum in the males of most *Blattidæ* are homologous with the abdominal appendages of the Thysanura, and yet the resemblance between the two is very striking; nor have any representatives of them yet been discovered in the females. Some months ago, while dissecting a species of *Blattidæ*, I detected at the extremities of the outer branches of the posterior bifid pair of appendages beneath the skin that was about to be cast, a small bud, with the skin that had shrunk away from it drawn out into a shrivelled and curled filament, and I dissected specimen after specimen of the same species, until I found the fully-evolved appendages shown in fig. 9, *a*. The appendages are reduced to mere rudiments in the eighth somite. (Fig. 7, *a*.) For further information see the rather full explanations of the accompanying woodcuts.

Fig. 4.

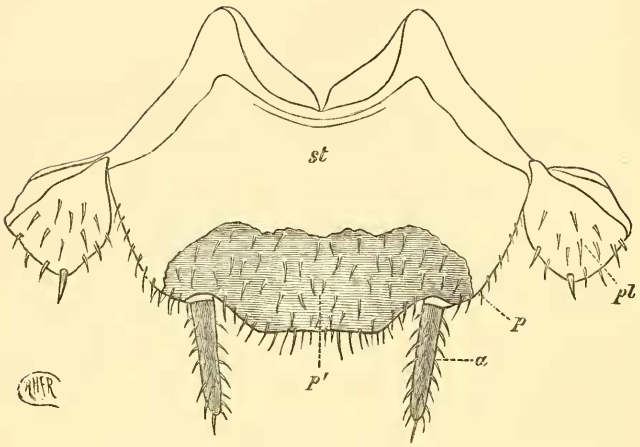

Fig. 4. '*Blatta*,' sp. The ninth sternum of the male : *st*, the sternum, which is colourless, or nearly so, and, when *in situ*, covered by that of the preceding somite ; the coloured and setose portion posterior to it represents the bases (protopodites) of the members which have coalesced with the sternum and with one another at *p'* in the middle line, where a narrow streak of lighter coloration than the surrounding chitine marks the junction ; *a*, the exopodites ; the endopodites (*b* in fig. 5) have been lost in the coalescence of the basal joints of the members with one another ; *pl*, lateral sclerites apparently homologous with those which carry the spiracles in the spiraculiferous somites of the body.

Fig. 5.

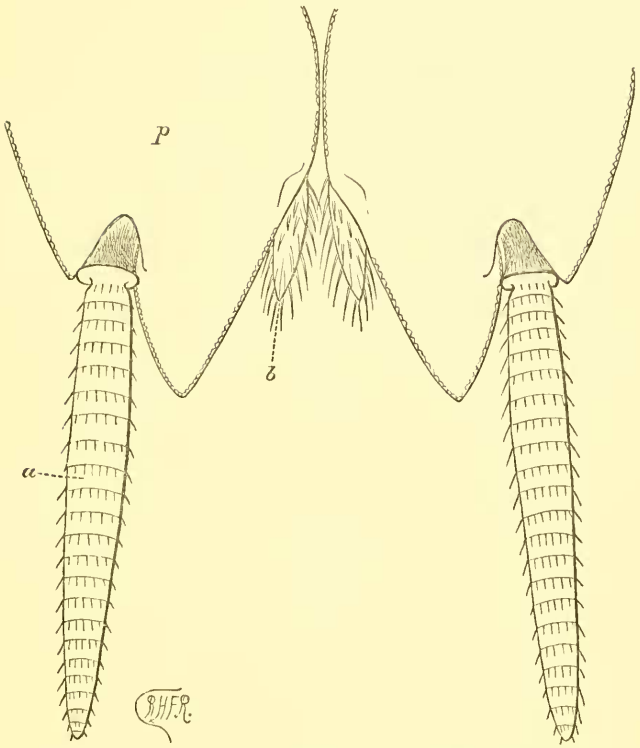

Fig. 5. *Lepisma*, sp. The appendages of the ninth abdominal somite in the male : *p*, the coalesced basal joints (protopodite) of one side carrying two branches, *a*, the exopodite, and *b*, the unmodified endopodites, which, with its fellow, answers to the posterior elements of the ovipositor in the female, but which is lost in the same segment in male *Blattidæ* in the coalescence of the two protopodites with one another and with the sternum (fig. 4); these endopodites are unquestionably represented in the preceding somite by a pair of whisps of long setæ, which whisps homologize with the more mesial of the two pairs of fringes of stiff yellow setæ in the somites anterior to the eighth, from which we may confidently infer that the ancestors of *Lepisma* possessed two-branched appendages, like those of the ninth, to all the somites of their abdomen.

The sternum and the basal parts of the protopodites are not shown in the figure.

Fig. 6.

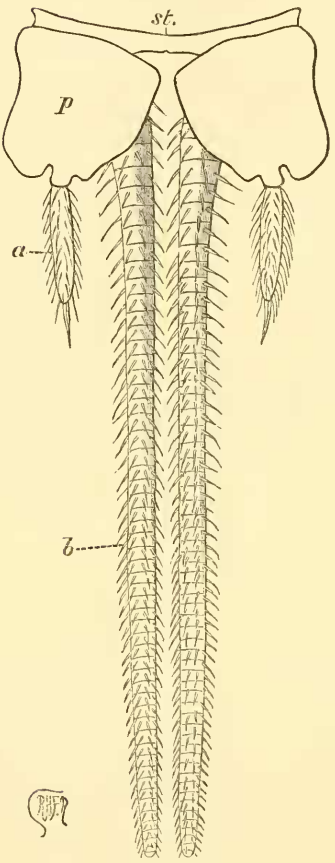

Fig. 6. *Machilis maritima*, ♀. The sternum with appendages of the eighth abdominal somite: *st*, sternum; *p*, the coalesced basal joints (protopodite) of the limb of one side supporting two branches, *a*, the exopodite, and *b*, the endopodite, here modified so as to form one of the four elements of the tubular ovipositor. The inner margins of the enlarged and produced exopoditic portions of the protopodites are represented as diverging from one another more than they do in the living insect to permit of the mode of insertion of the endopodites being seen.

Fig. 7.

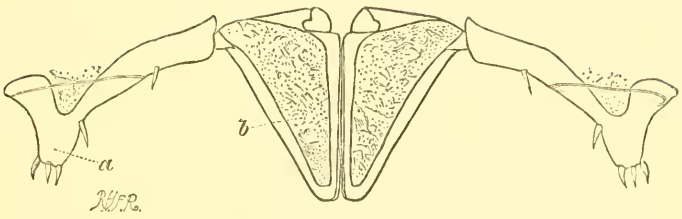

Fig. 7. '*Blatta*,' sp. Appendages of the eighth sternum or anterior gonapophyses, in a specimen of the apterous female which appears to have undergone the last ecdysis. No part of the sternum (*st*) is shown in the figure; *b*, the setulose endopodites (knife-blade-like processes of Prof. Huxley), answering to the two long, many-jointed, and setulose styles forming the anterior elements of the ovipositor (*b*, *b*) in *Machilis;* in an earlier stage than that here figured they are distinctly two-jointed; they are articulated, not to the sternum, but to the inner ends of two pieces (the protopodites) which are attached to the sternum and are all but confounded with it; externally to the endopodites two short and depressed teat-shaped and sparsely setulose appendages, which evidently homologize with the exopodites of *Machilis*, and the discovery of which, and of their homologues in the succeeding somite, establishes the perfect morphological identity of the gonapophyses of female *Blattidæ* with the ovipositor of *Machilis* and of *Lepisma*, are attached to the posterior margins of the same two pieces, from which they are marked off by a faint circumferential inflection of the integument. In the earlier stage above referred to, the endopodites at their bases as distinctly curve inwards and backwards as the homologous parts in *Machilis* are seen to do in fig. 6. The dotting is intended to represent the epidermis and subjacent tissues, which have contracted in the spirit and shrunk away from the chitinous cuticle.

Fig. 8.

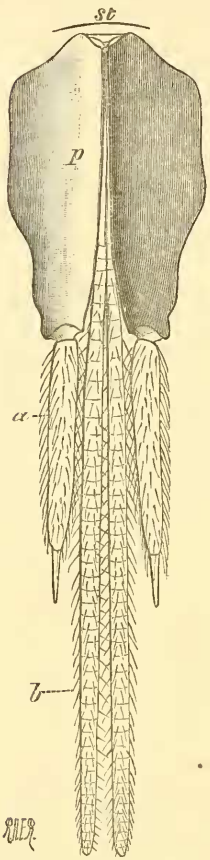

Fig. 8. *Machilis maritima*. The sternum with appendages of the ninth abdominal somite in the female: *st*, sternum; *p*, the coalesced basal joints (protopodite) of one of the limbs, supporting, as in the preceding somite, two branches, *a*, the exopodite, and *b*, the endopodite, modified so as to form the long, jointed, and setulose posterior elements of the ovipositor and articulated to the base of the protopodite on the upper (dorsal) side of this, which is produced into a large operculiform plate that meets its fellow in a straight suture in the middle line and carries at its extremity an exopodite. In female *Blattidæ*, the great boat-shaped seventh sternum does duty for the operculiform productions of the exopoditic portions of the protopodites of both the genital somites in *Machilis*.

Fig. 9.

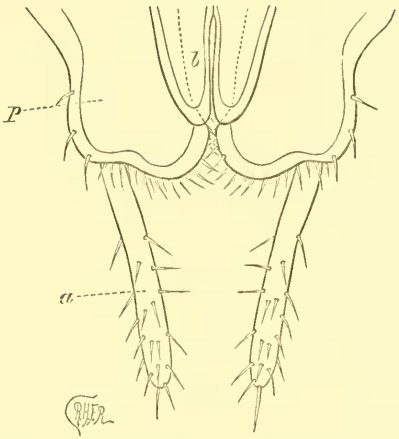

Fig. 9. '*Blatta*,' sp. Appendages of the ninth abdominal somite, or posterior gonapophyses, of the female, drawn from the same specimen as fig. 7, and viewed from the dorsal or upper side, so as to show the triangular endopodites (*b*) answering to the posterior elements of the ovipositor in *Machilis* and *Lepisma*; *a*, the exopodites, which are as firmly chitinized and as deeply coloured as, but relatively even larger than, the obviously homologous 'styles' of many male *Blattidæ* (fig. 4, representing the sternum, with appendages of the ninth abdominal sternum in the male of the same or an allied species); *p*, the coalesced basal joints (protopodite) of the biramous limb of one side: the part of this that carries the exopodite is produced much as in *Machilis* (fig. 8), but instead of meeting its fellow of the opposite side in the middle line, so as to conceal from their origin the endopodites that are attached to its own and to its fellow's base, meets its fellow only at the inner extremity, where it is expanded and strongly spined, so as to resemble, and, perhaps, to serve as, a forceps; the dotted lines represent the inner margins of these produced exopoditic portions of the protopodites as seen from the ventral or under side, in which view the endopodites can only be seen meeting in a straight median suture in the triangular hiatus bounded by the margins here shown in dotted outline.

In a much earlier stage than the one here depicted, the exopodites are represented by minute buds only, which increase with each successive ecdysis. In many *Blattidæ* which are much more modified than this, as, for instance, in *Panesthia Javanica*, no vestiges of exopodites appear to be present in either sex, at any stage, on either the eighth or the ninth abdominal sternum

The sternum is not shown in this figure.